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Revision of the Ascidian Genus *Herdmania* (Urochordata: Ascidiacea) Inhabiting Japanese Waters

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The pyurid ascidian genus Herdmania Lahille, 1888 has been known in Japanese waters by a single species, H. momus (Savigny, 1816), with two later proposed taxa treated as its junior synonyms. My detailed examination of many museum specimens, including most of those recorded from Japan in earlier publications and name-bearing types of the species to be compared, and also of newly collected material, reveals that these waters are inhabited by the following seven species: H. momus (Savigny), s. str.; H. pallida (Heller, 1878), for which a lectotype is designated; H. japonica (Hartmeyer, 1909), based on examination of syntypes, with Rhabdocynthia siphonalis Oka, 1933 as a probable junior synonym; H. mauritiana (Drasche, 1884) (=H. insolita Monniot and Monniot, 2001), based on examination of the holotype of the former; H. subpallida sp. nov.; H. kiiensis sp. nov.; and Herdmania sp. (=H. momus, sensu Millar 1975). A tabular comparison of these Japanese species, together with *H. curvata* Kott, 1952 (=*H. contorta* Monniot, 1992, syn. nov.), *H.* inflata (Van Name, 1918), and H. polyducta Monniot and Monniot, 1989, is compiled on the basis of a reexamination of the name-bearing types or paratypes of these latter species. Specific delimitations are based largely on the detailed structure of the gonads.

Key Words: Herdmania, Ascidiacea, taxonomy, new species, Japan.

Introduction

The ascidian genus *Herdmania* of the family Pyuridae was established by Lahille (1888) in his "Tableau des genres" for species having "spicules échinés", i.e., unique, peculiar, calcareous, needle-like spicules covered with "rings of minute appressed spines" (Van Name 1945: 341). For accounts of spicule morphology, mineralogy, and formation see Lowenstam and Abbott (1975), Lambert and Lambert (1987), and Lambert (1992); they are called "burred spicules" in the present paper. Although the original description of *Herdmania* lacked any mention of nominal species included therein, the generic name is available from Lahille's (1888) work according to Articles 11 and 12 of the International Code of Zoological Nomenclature, 4th ed. (International Commission on Zoological Nomenclature 2000). This genus remained unused for a long time, lost in the complicated history of the taxa comprising such genera as *Pyura* Molina, 1782, *Rhabdocynthia* Herdman, 1891, and *Halocynthia* Verrill, 1879; however, it was resurrected by Das (1936)

with a wide range of included species. Van Name (1945) seems to have been the first to adopt the currently prevailing restricted usage of the genus *Herdmania*, regarding *Cynthia momus* Savigny, 1816 as its only valid included species, with many junior synonyms as summarized by Michaelsen (1919). Since then, *Herdmania momus* (Savigny), or *Pyura momus* (Savigny) in another system, has been regarded as the only valid species with these unique spicules among the known ascidians. It has been considered to have a very wide tropical to temperate geographical (and even eurybathyal) distribution by many taxonomists (e.g., Tokioka 1953; Millar 1960; Kott 1985; Nishikawa 1991); sometimes it has been subdivided at the rank of form or variety. Some species of the genus *Pyura*, lacking such spicules, were once also included in the genus *Herdmania*, mainly on the basis of the similar number, position, and structure of the gonads (for details see Tokioka (1965) and below); however, this wider definition was not generally followed.

Recently, the above-mentioned monotypic classification of the genus *Herdmania* was adopted as a starting point for Monniot's (1992, 2002) and Monniot and Monniot's (1989, 1991, 2001) works, in which seven additional species were described in the genus. Furthermore, Degnan and Lavin (1995) revealed significant molecular and embryological differences between the two allopatric "morphological forms" of *H. momus* ("forma *grandis*" and "forma *curvata*") on the eastern coast of Australia; the latter has recently been called *H. curvata* Kott, 1952 (e.g., Degnan and Johnson 1999).

It seems, however, that *H. momus* in the limited sense of Monniot (1965, 1992) and Monniot and Monniot (1987) has a gonadal structure different from that clearly figured in Savigny's (1816) original description, as Monniot and Monniot (2001) recently pointed out. For a better understanding of the diversity and pattern of speciation in this genus, it is necessary to clearly delimit *H. momus* and simultanously provide a taxonomic and nomenclatural revision of the many nominal species hitherto synonymized with it.

I tried to find the name-bearing type of *Cynthia momus*, collected during Napoleon's Egyptian campaign (for some details, see Bouchet and Danrigal 1982) from the "golfe de Suez" (Savigny 1816) in the northernmost part of the Red Sea. I also tried to collect or obtain specimens from the type locality. Unfortunately, these efforts have so far been unsuccessful. Instead, I examined many older specimens (including name-bearing types of some other nominal species) from the Gulf of Suez and other places deposited in several European museums; most of the previous descriptions lack meaningful information as to the gonadal structure, which is where the fundamentally most significant diagnostic characters appear to lie.

On the basis of the results thus far gained, based on examination of much museum material and also newly collected specimens, here a taxonomic revision is presented of the Japanese ascidians belonging to this genus, so far referred only to the single species *H. momus*. This is accompanied by taxonomic delimitations and nomenclatural revisions of *H. momus* and *H. pallida* (Heller, 1878), the latter having usually been regarded as the oldest junior synonym of the former, and descriptions of two new species. In all, the Japanese *Herdmania* fauna is shown to consist of seven species. Some results of the present study were presented at the 72nd Annual Meeting of the Zoological Society of Japan (Nishikawa 2001).

Names of the museums where the examined specimens are deposited are abbreviated as follows: AMS (Australian Museum, Sydney), MNHM (Muséum na-

tional d'Histoire naturelle, Paris), NHML (The Natural History Museum, London), NHMW (Naturhistorisches Museum Wien), NSMT (National Science Museum, Tokyo), NUM (The Nagoya University Museum), OCUT (Oka Collection of the University of Tsukuba), USNM (National Museum of Natural History, Smithsonian Institution), ZMA (Zoölogisch Museum, University of Amsterdam), ZMB (Museum für Naturkunde der Humboldt-Univertität zu Berlin), ZMK (Zoologisk Museum, Copenhagen), and ZMUH (Zoologisches Museum, Universität Hamburg).

Brief Taxonomic History of Herdmania in Japanese Waters

The first record of the genus *Herdmania* (as defined above) in Japanese waters was made by Hartmeyer (1906) as the "japanisches Form" of *Halocynthia pallida* (*Pyura pallida* f. *japonica* Hartmeyer, 1909) from "Tokiobucht" at a depth of 600 m. Then, *Rhabdocynthia siphonalis* Oka, 1933 was established for specimens with extremely elongated siphons dredged off Misaki, Sagami Bay, 150–250 m deep (Oka 1933). Tokioka (1953) synonymized these two with *H. momus*, reducing them to the level of forma. Since then, this genus has been considered to be represented only by *H. momus* in Japanese waters (e.g., Tokioka 1967; Millar 1975; Nishikawa 1991).

Nishikawa (1991: 137) found in specimens of *Herdmania* from the Sea of Japan "a thin rectangular membrane issu[ing] from the free surface of the proximal or middle part of [the] thick [,] short oviduct, and extending far beyond its opening located at its distal extremity" and "testicular follicles with many short ducts [termed "ejectors" in the present study] located over the most part of [the] mesial surface of [the] gonad." Although these specimems were identified as *H. momus*,

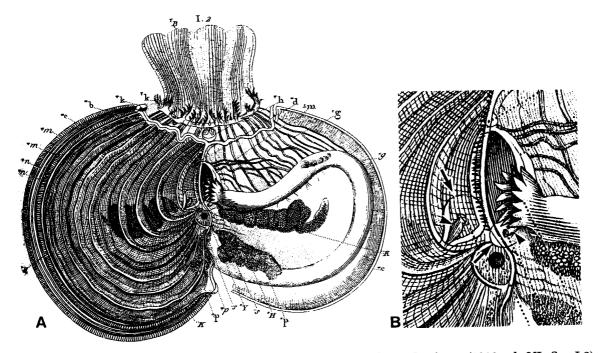


Fig. 1. Original drawings of *Herdmania momus* (Savigny) from Savigny (1816, pl. VI, fig. I.2). A, ventrally opened specimen; B, central part of A, enlarged to show round hood (arrow) encompassing terminal free part of oviduct (arrowhead), latter opening into dorsal part of peribranchial cavity on each side.

Nishikawa (1991) made no mention of two facts: 1) a similar membranous structure is mentioned in the original description of *Cynthia momus*, which states (Savigny 1816: 144) that each ovary is "terminé chacun par un cornet membraneux, duquel sort le bout du tube d'émission" (= each terminated by a membranous horn, from which the extremity of the emission tube projects; see Fig. 1); 2) the specimens from the Sea of Japan are different from *H. momus* defined by Monniot (1965) and Monniot and Monniot (1987), whose clear figures show each gonad furnished with its own aperture of the vas deferens located close to the orifice of the oviduct, unaccompanied by any accessary organs. These differences should not have been regarded as intraspecific variation, as Nishikawa (1991) did. Nishikawa (1992, 1995) subsequently suggested the existence of two or more species of *Herdmania* around the Japanese Islands.

Another Japanese species, *Pyura mirabilis* (Drasche, 1884), which lacks the characteristic burred spicules, was also included in *Herdmania* by Tokioka (1965) mainly on the basis of the similar number, position, and structure of the gonads, and this classification was followed by Tokioka (1967), Rho (1971), and Nishikawa (1991), among others. Although this treatment is not adopted in the present study, it doesn't mean that the phylogeny of *Herdmania* and related genera is fully understood. Future molecular analyses are expected to prove the monophyly of the genus *Herdmania*.

All seven species to be described here have elongate burred spicules that are similar among themselves (Figs 6, 10).

Taxonomic Descriptions

Herdmania momus (Savigny, 1816) (Figs 1, 2A, 3–4; Table 1)

Cynthia momus Savigny, 1816: 90–92, 143–144, 217, pl. 6, figs 1.1–1.3 (the name-bearing type unexamined).

Cynthia papietensis Herdman, 1882: 143–145, pl. 17, figs 11–16 (*partim*, fig. 10 of pl. 17 excluded). **Syn. nov**.

Confirmed previous records

Herdmania momus: Van Name 1952: 217 (partim); Tokioka 1967: 205–206 (partim); Nishikawa 1980, table 1 (partim); 1986: 176 (partim); 1991: 137 (partim); 1992: 2–3, fig. 1; Monniot 2002: 111–113, figs 35c, 36 (based only on literature).

Pyura momus f. typica: Michaelsen 1919: 31, 54 (partim). [Nec Michaelsen, 1918] Pyura momus f. kyamanensis: Michaelsen 1919: 31 (partim, paralectotypes; for taxonomy of lectotype, see section on Herdmania pallida below).

Specimens examined. *Cynthia papietensis*: lectotype (for its designation, see Appendix herein) collected from Papiete (i.e. Papéeté) Harbor, Tahiti, Society Isls, 10 ftms (i.e. 18.2 m), "Challenger" Exp., 28 Sept. 1875, 20 mm long, one of 5 syntypes of NHML 1887.2.4.63–67, labeled as *H. momus* f. *papietensis* Herdman.

Pyura momus f. *typica* of Michaelsen (1919) from the following localities in the Red Sea: 1) Suez, collected by E. Bannwarth in 1914, ZMUH T981+T998, 4 inds 24–67 mm long, with 2 intact ones left unexamined; 2) Suez, ZMUH T316, 3 inds 20–33 mm

long, with 2 badly damaged specimens and an intact one left unexamined; 3) Suez, ZMB 2922, 1 ind. 54 mm long, with 2 intact ones left unexamined; 4) Sherm Habban, ZMUH T1038, "Pola" Exp., 12 (from the label, instead of "13" in the cited paper) Jan. 1896, 1 ind. 20 mm long; 5) Sherm Habban, NHMW Mollusken Sammlung Nr. 55599, "Pola" Exp., 12 [ditto] Jan. 1896, det. by Michaelsen, 2 intact inds 13–18 mm long and a 24 mm long ind. already opened and attached to a glass plate; 6) Jiddah (Djeddah), "Pola" Exp., ZMUH T1039, 16 (on the label, instead of "10" in the cited paper) Dec. 1895, 2 inds 40 mm long; 7) Jiddah (Djeddah), "Pola" Exp., ZMUH T1053 (part), 4 inds 34–43 mm long, with the 22.5 mm long *H. pallida* (see below) excluded.

Pyura momus f. *kyamanensis* Michaelsen, 1919: 2 paralectotypes (for their designation, see Appendix herein), fragmented individuals with mature gonads in glass vials numbered 28 and 33, ZMB 3315 (part), collected from Umm el Kyaman (Umm el Jerman), southern end of Gulf of Suez, by R. Hartmeyer, 18–20 Jan. 1902.

Herdmania momus of Van Name (1952): NHML 1950.2.27.7, 1 specimen somewhat deteriorated probably due to drying in the past, "Manihine" Exp., St. A1, shore of Firaun Is., Gulf of Aquaba, 31 Dec. 1948.

Herdmania momus of Tokioka (1967, part): USNM 11702, exchange from Imperial Univerity of Tokyo (Acc. No. 52210), received 7 Dec. 1910, from Mogi ("Moji" in the cited paper), near Nagasaki, Japan, E. S. Morse coll., 5 inds (3 according to Tokioka (1967), but 2 more attached firmly to others) 19–30 mm long.

Herdmania momus of Nishikawa (1980, part) from Kii Peninsula: NUM-Az0010, Shinden, Nigijima-cho, Mie Pref., several meters, 29 July 1979, T. Nishikawa coll., 1 ind. 23 mm long; NUM-Az0011, Cape Anori-zaki, Mie Pref., several meters, 24 July 1979, T. Nishikawa coll., 1 ind. 36 mm long; NUM-Az0012, Hoomon-no-hama, Cape Daio-zaki, Mie Pref., several meters, 25 July 1979, T. Nishikawa coll., 6 inds 25.5–32.5 mm long, living together with H. pallida (Heller, 1878); NUM-Az0013, northern beach of Seto Marine Biological Laboratory of Kyoto Univ. (SMBL), Tanabe Bay, Wakayama Pref., 12 May 1975, T. Kuwamura coll., 2 inds 15.5–18.5 mm long; NUM-Az0014, Toshima Is., Tanabe Bay, 8 m, 2 June 1975, T. Kuwamura coll., 2 inds 29–35 mm long; NUM-Az0015, northern beach of SMBL, Tanabe Bay, 30 June 1977, R. Fukao coll., 2 inds 30–37 mm long; NUM-Az0016, Tanabe Bay, 30–80 m, 4–5 June 1979, dredged by T. Imaoka, 2 inds 24.5–30.0 mm long; NUM-Az0017, Tanabe Bay, depth unknown, 11 July 1977, dredged by staff of SMBL, 1 ind. 21 mm long.

Herdmania momus of Nishikawa (1986, part) and Nishikawa (1991, part) from the Sea of Japan: NUM-Az0018, off Uchiura Bay, Fukui Pref., 40 m, 11 June 1980, dredged by T. Yasuda, 1 ind. 19 mm long; NUM-Az0019, 36°10.17′N, 133°13′E, off Oki Isls, Shimane Pref., 47–55 m, 9 Sept. 1985, T. Nishikawa coll., 15 inds 4–24 mm long; NUM-Az0020, 36°10.20′N, 133°14–15′E, off Oki Isls, 40–55 m, 10 Sept. 1985, T. Nishikawa coll., 6 inds 6.0–18.5 mm long; NUM-Az0021, 36°09.66′N, 133°17.22′E, off Oki Isls, 30–35 m, 11 Sept. 1985, T. Nishikawa coll., 2 inds 15–20 mm long; NUM-Az0022, 36°09′N, 133°16′E, off Oki Isls, 30–45 m, 11 Sept. 1985, T. Nishikawa coll., 1 ind. 11.5 mm long; NUM-Az0023, 36°10.29′N, 133°13.52′E, off Oki Isls, 35–45 m, 12 Sept. 1985, T. Nishikawa coll., 10 inds 4–17 mm long; NUM-Az0024, 36°08.53′N, 133°14.36′E, off Oki Isls, 35–45 m, 12 Sept. 1985, T. Nishikawa coll., 1 ind. 13 mm long.

New collections from Sagami Bay: NUM-Az0025, Manazuru, 5 m, 20 Dec. 1993, I. Soyama coll., 3 inds 18–22 mm long; NUM-Az0026, Manazuru, 5 m, 20 Dec. 1993, I. Soyama coll., 1 ind. 30 mm long; NUM-Az0027, Ichiban-no-ne, Izu Marine Park, Izu Pen., ca. 10 m, 30 Sept. 1991, T. Nishikawa coll., 3 inds 22–28 mm long; NUM-Az0028,

Futo Fisheries Port, Izu Pen., 6 m, 30 Sept. 1991, T. Nishikawa coll., 1 ind. 29 mm long; NUM-Az0029, Futo Fisheries Port, Izu Pen., 10 m, 1 Oct. 1991, T. Nishikawa coll., 1 ind. 23 mm long; NUM-Az0030, buoy in Nabeta Bay, Shimoda, 12 June 1997, K. Ueda coll., 2 inds 39–48 mm long; NUM-Az0031, rope of buoy in Nabeta Bay, Shimoda, 23 Oct. 1992, Y. Hirose coll., 3 inds 27–28 mm long (+3 inds for thin sections); NUM-Az0032, Nabeta Bay, Shimoda, 3 m, 11 June 1997, T. Nishikawa coll., 2 inds 29–43 mm long; NUM-Az0033, Nabeta Bay, Shimoda, detached from slide glass immersed in surface water and cultured by F. Nakaya, 11 June 1997, 1 ind. 30 mm long; NUM-Az0034, Nabeta Bay, Shimoda, detached from slide glass immersed in surface water and cultured by F. Nakaya, 11 June 1997, 1 ind. 30 mm long.

New collections from other regions of Japan: NUM-Az0035, Sugashima Is., Ise Bay, Mie Pref., from pier of Sugashima Marine Biological Laboratory of Nagoya Univ. (Sugashima MBL), 12 June 1980, T. Nishikawa coll., 4 inds 12–30 mm long; NUM-Az0036, Sugashima Is., Ise Bay, from pier of Sugashima MBL, 23 Oct. 1980, T. Nishikawa coll., 6 inds 12-24 mm long; NUM-Az0037, shore of Senjo, Sugashima Is., Ise Bay, 22 Nov. 1980, T. Nishikawa coll., 2 inds 20–26 mm long; NUM-Az0038, buoy set off Sugashima MBL, Sugashima Is., Ise Bay, 24 Dec. 1980, T. Nishikawa coll., 3 inds 10-16 mm long; NUM-Az0039, Sugashima Is., Ise Bay, from pier of Sugashima MBL, 21 Jan. 1981, T. Nishikawa coll., 10 inds 11-27 mm long; NUM-Az0040, Sugashima Is., Ise Bay, from pier of Sugashima MBL, 18 Feb. 1981, T. Nishikawa coll., 2 inds 11-18 mm long; NUM-Az0041, Sabiura, Kushimoto-cho, Wakayama Pref., Kii Pen., 2-5 m, 20 Mar. 1988, T. Nishikawa coll., 5 inds 18-28 mm long; NUM-Az0347, Hatakejima Is., Tanabe Bay, Wakayama Pref., intertidal, 28 Apr. 1998, T. Nishikawa coll., 1 ind. 18 mm long; NUM-Az0042, Ikata-cho, Ehime Pref., Seto Inland Sea, 15.1 m, 27 May 1996, M. Ootani coll., 1 ind. 24 mm long, living together with H. japonica (Hartmeyer, 1909); NUM-Az0043, Kagoshima Bay, depth unknown, Dec. 1984, J. Tsukahara coll., 1 ind. 12.5 mm long; NUM-Az0044, Motobu-cho, Okinawa Is., Okinawa Pref., from pier, 1–2 m, June 1987, J. Kobayashi coll., 1 ind. 36 mm long; NUM-Az0045, Kerama Isls, Okinawa Pref., shore, 11 Mar. 2000, Y. Hirose

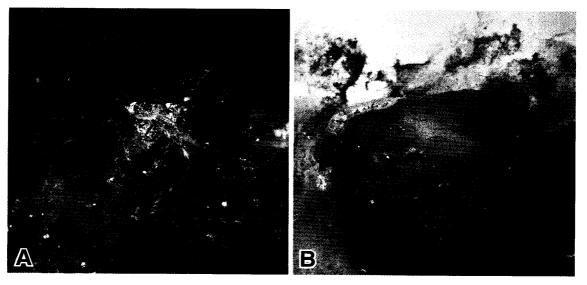


Fig. 2. Underwater photographs of *Herdmania momus* (Savigny) (A) in Futo Harbor and H. pallida (Heller) (B) in Shimoda, western coast of Sagami Bay.

coll., 2 inds 27–37 mm long; NUM-Az0046, Kuroshima Is., Okinawa Pref., several meters, 27 June 1988, T. Nishikawa coll., 1 ind. 24 mm long.

Description. Body soft, up to 67 mm long (smallest mature specimen 10 mm), oval in outline, more or less flattened laterally. Both siphons distinct; atrial one rarely somewhat elongated, though much less developed than in "*Rhabodocynthia siphonalis*" (see the section on *H. japonica* below). Surface sometimes covered to various degrees with sand grains, shell fragments, coral debris, hydrozoan or ascidian colonies, etc. Tunic very thin, like paper, almost transparent and white even in larger specimens; bivalves (probably *Musculus* sp.) sometimes embedded in it. In life, reddish mantle body recognizable through tunic, with red ovarian eggs and orange testicular follicles (Fig. 2A). Density of burred spicules in tunic, mantle, and visceral tissues varying considerably among individuals, but often very high.

Tentacles of several sizes, 20–30 in number, branched in 3–4 orders in larger specimens. Branchial folds often right-dominant in number and degree of development, and number of folds roughly correlated positively with body length (Table 1). Ciliated groove usually simple C-shaped and open anteriorly, with both horns inrolled in larger specimens (Fig. 4A). Dorsal languets distinct. Atrial velum as very low crest or divided into many membranous projections; no atrial tentacles. Stomach covered densely with hepatic lobules. Intestinal loop very wide. Anal margin always cut into many elongated lobules (Fig. 4B).

Single gonad on each side; left one in intestinal loop along latter's dorsal branch; exceptionally, 2 small gonads only on right in 41 mm long specimen ZMUH T1053 from Red Sea. Each gonad large and elongated; left and right ones similar to each other in structure. Testicular follicles sinuate over mesial surface of ovary

Table 1. Number of branchial folds on each side in some specimens of *Herdmania momus* examined herein.

Body Length (mm)	Number of folds*		
	on left side	on right side	
6	7+1	7+1	
10	8+1	8+1	
17	8+1	9	
18	8	9	
18	9	9	
19	8	8 + 1	
23	8+1	8 + 1	
24	8	8 + 1	
27	9+1	9+1	
30	8+1	8+1	
35	9+1	10	
37	9 + 1	9 + 1	
40	8 + 1	$8\!+\!1$	
43	9	9+1	
48	9	9+1	
61	9	9	

^{*} Shown as (no. of complete folds)+(no. of incomplete, only anteriorly detectable folds).

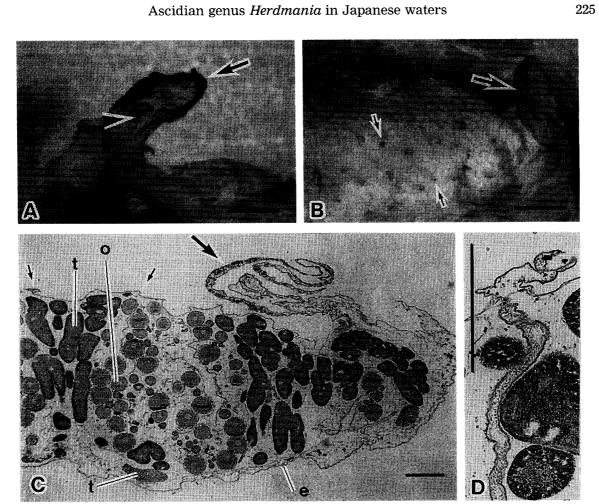
(Fig. 4B) in specimens from Suez and Jiddha (ZMUH T981+T998, T1053 (part), T1039), while sinuate arrangement of testis more or less obscure in specimens from Suez (ZMUH T316); follicles uniformly and completely covering whole surface of axial ovary in Suez specimens ZMB 2922 and ZMB 3315 (part). Such variation also discernible in Japanese specimens, although markedly sinuate arrangement of testis detected very rarely in specimens from Tanabe Bay (NUM-Az0013 and 0014); in most Japanese specimens (and lectotype of *Cynthia papietensis*), testicular follicles uniformly covering most or whole of mesial surface of axial ovary. Mesial surface of testicular follicles always densely set with fine, short but erect ejectors (Fig. 3B, D). Very unusually, prominent protuberance probably representing additional branch of oviduct detected on opposite side of hood to terminal free part of oviduct (Fig. 4C) in 18 mm long specimen from Sabiura, Kii Peninsula (NUM-Az0041). Testicular follicles often extending to bottom layer of gonad (Fig. 3C).

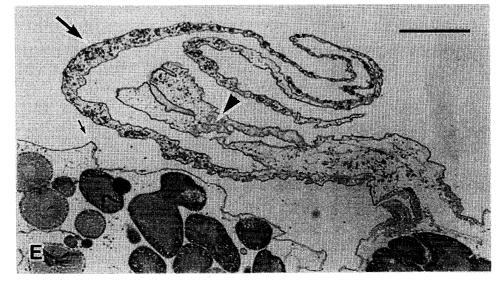
Ovary opening through aperture (sometimes bilobed, but usually smooth-margined) on top of elongated terminal free part of oviduct projecting from mantle wall. Free part of oviduct shrouded incompletely by extensive conical hood made of very thin, fragile, fan-shaped membrane with smooth and often inrolled free edge (Figs 3A, E, 4B, C); free edge representing long, circular margin of hood orifice. Proximal end of hood narrow and encircling base of free part of oviduct completely or only mesially.

Remarks. Some specimens from Suez and Tanabe Bay in the present material have a sinuate testis and a "cornet membraneux" (see above; termed "hood" herein) around the terminal free part of the oviduct. These features agree with the original description of Cynthia momus (i.e. Herdmania momus) (original figure reproduced in Fig. 1), which was based on "1 à 2 pouces" (=ca. 2.5–5.0 cm) long specimens from the Gulf of Suez (Savigny 1816: 143). Therefore, the mentioned specimens may safely be referred to H. momus in its original sense. They have fine ejectors of the testicular follicles, which may have been missed in the original description. This supposition is supported by the statement of Monniot and Monniot (2001: 343) that in "typical Herdmania momus all characters [i.e., a contorted ovary and multiple openings of small sperm ducts, a lobed anus [were] confirmed by a reexamination of old material from Suez." (see also Monniot 2002). The sinuate arrangement of the testis may well be an unstable feature in this species, as shown by its partial or complete lack of expression in specimens NHUH T316, ZMB 2922, and ZMB 3315 (part), which are otherwise similar to specimens with a sinuate testis.

The sinuate arrangement of the testis over the mesial surface of the ovary in

Fig. 3. Gonads of *Herdmania momus* (Savigny) collected from Nabeta Bay, Shimoda (NUM-Az0031). A, side view from orifice end of gonad, hood (arrow) surrounding base of terminal free part of oviduct (arrowhead), artificially stained; B, mesial view of gonad, near orifice end, showing hood (large arrow) around oviduct and fine, erect ejectors (small arrows) over mesial surface of testicular follicles, artificially stained; C, E, transverse sections of gonad near orifice end showing hood (large arrow), terminal free part of oviduct (arrowhead), ejectors (small arrows), ovarian eggs (o), and testicular follicles (t) sometimes reaching outer wall of mantle (=epidermis (e)); D, longitudinal section of ejector projecting from gonadal surface with its duct among testicular follices. Scales 1 mm.





some specimens of *H. momus* is highly reminiscent of the original descriptions of *Herdmania momus* var. *curvata* Kott, 1952 (=*H. curvata* Kott, 1952) recorded from Queensland, Australia (Kott 1952: 282–283, text-fig. 129) and *H. contorta* Monniot, 1992 from New Caledonia (Monniot 1992: 18–19, text-figs 6B, 7); these two species may be comparable to *H. japonica* rather than to *H. momus*, because *H. curvata* and *H. contorta* usually have a membranous flap issuing from the mesial lip of the oviduct orifice, instead of a hood as seen in *H. momus*. A "hood" is a membrane issuing from the base of the free terminal part of the oviduct to encompass that part widely and incompletely, with the membrane's edge forming the large opening of the hood (see Figs 3, 4, 8). A "flap", on the other hand, projects from the mesial lip of the usually elongated orifice of a completely or almost sessile oviduct (see Figs 7, 9C, E). No intermediates between "hood" and "flap" thus defined have been observed. This difference might be regarded as too subtle a character for distinguishing species, but I believe it can be used that way, at least as a provisional working

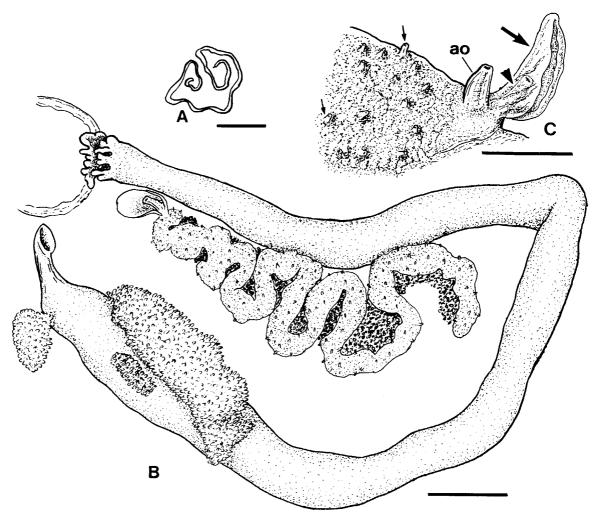


Fig. 4. Herdmania momus (Savigny) from Suez (A–B, ZMUH T981+T998) and Kushimoto (C, NUM-Az0041). A, ciliated groove of 61 mm long specimen; B, alimentary canal and gonad of same specimen, with erect ejectors over gonad; C, orifice end of aberrant gonad with supernumerary thick branch of oviduct? (ao), as well as many fine ejectors (small arrows), near hood (large arrow) and oviduct (arrowhead). Scales 1 mm for A, C, 5 mm for B.

hypothesis.

In having numerous erect ejectors of the testicular follicles, *H. momus* is very similar to *Pyura polyducta* Monniot and Monniot, 1989 (Monniot and Monniot 1989: 237–238, text-fig. 4, pl. I, figs F–G), which has been included recently in the genus *Herdmania* (see Monniot 1992; Monniot and Monniot 2001). My reexamination of two paratypes of *P. polyducta* from the Philippines, collected at a depth of 70–76 m (MNHN S2PYU244), revealed another similarity: the oviduct orifice of each gonad is furnished with a membranous flap (the holotype MNHN S2PYU243 remains undissected). In this case, the flap consists of a large, thin, spade-shaped membrane issuing from the mesial lip of the oviduct orifice except in the right gonad of the smaller paratype, in which the structure is reduced to a minute projection. In *H. momus*, on the other hand, a membranous hood surrounds the free terminal part of the oviduct. Furthermore, the ovary in these paratypes of *H. polyducta* is only fringed with testicular follicles, while it is covered with them in *H. momus*. These two species are thus considered distinct.

Confirmed distribution. Japanese waters, intertidal to 55 m: Sea of Japan coast (Fukui Pref. and Oki Isls), Sagami Bay, Kii Peninsula, Seto Inland Sea, Kagoshima Bay, and Rhykyu Isls. Tahiti, 18 m. Red Sea including Gulfs of Suez and Aquaba, Gulf of Aden, Lebanon, Cyprus, and Mozambique, depth unknown.

Herdmania pallida (Heller, 1878) (Figs 2B, 5)

Cynthia pallida Heller, 1878: 96–97, pl. 3, figs 17–18 (partim).

Cynthia pallida var. billitonensis Sluiter, 1885: 183–186, pl. 1, fig. 6, pl. 4, figs 1–11. [Syn. by Monniot (2002)]

Cynthia rosea Sluiter, 1887: 264–266, pl. 1, fig. 9, pl. 3, figs 7–8. [Syn. by Monniot (2002)] Pyura momus f. kyamanensis Michaelsen, 1919: 31, 53 (partim, lectotype only; for its designation see Appendix herein). [Syn. nov.]

Rhabdocynthia ceylonica Herdman, 1906: 309–311, pl. 3, figs 1–19. [Syn. nov.]

Pyura (Rhabdocynthia) pallida f. formosae Michaelsen, 1908: 267–271. [Syn. nov.]

Confirmed previous records

Pyura momus f. pallida: Hartmeyer and Michaelsen 1928: 444 (partim).

Halocynthia pallida: Michaelsen 1905: 78–85 (partim, fig. 11 of pl. 4 excluded).

Herdmania pallida?: Monniot and Monniot 2001: 341–343, figs 104, 129F (based only on literature).

Herdmania pallida: Monniot 2002: 113–115, figs 35D, 37 (do.).

Herdmania (Rhabdocynthia) pallida: Das 1936: 1–103, text-figs 1–64 (do.).

Cynthia papietensis: Herdman 1882: 143–145, pl. 17, figs 10–16 (fig. 11 of pl. 17 excluded) (*partim*, a paralectotype, designated in Appendix herein).

Pyura (Herdmania) ceylonica: Michaelsen 1911: 178–179. [Nec Herdman, 1906]

Herdmania momus: Van Name 1952: 217 (partim); Tokioka 1967: 205–206 (partim); Monniot 1992: 16–17, text-fig. 6A (based only on literature); Nishikawa and Tokioka 1975: 222; Nishikawa 1980, table 1 (partim); Nishikawa 1991: 137 (partim); Nishikawa 1992: 2–3, fig. 1. [Nec Savigny, 1816]

Pyura momus f. typica: Michaelsen 1919: 31 (partim). [Nec Michaelsen, 1918]

Pyura momus: Monniot 1965: 102-107, text-figs 33-34; Monniot 1983: 1022-1023, text-

fig. 1A; Monniot and Monniot 1987: 122–123, text-fig. 48 (based only on literature). [Nec Savigny, 1816]

"Typischen Pyura pallida": Michaelsen 1908: 269 (partim).

Specimens examined. *Cynthia pallida*: lectotype (for its designation, see Appendix herein), part of ZMB 704, collected from Mauritius by Möbius, 31 mm long, left and right halves of mantle body separated completely.

Cynthia pallida var. *billitonensis*: syntypes, ZMA TU 895, collected from Billiton Is., Java Sea, 4 ftms (i.e. 7.3 m), 4 inds 28–48 mm long.

Cynthia rosea: part of syntypes, ZMA TU 400, collected from Bay of Batavia (i.e. Jakarta), Java Sea, by C. Ph. Sluiter, 2 inds 16–23 mm long; mantle body probably of 23 mm long specimen lacking intersiphonal area and dorsal complex.

Pyura momus f. *kyamanensis*: lectotype (for its designation, see Appendix herein), part of ZMB 3315, fragmented individual (body length unknown) in glass vial numbered "26", collected in Umm el Kyaman (Umm el Jerman), southern end of Gulf of Suez, by R. Hartmeyer, 18–20 Jan. 1902.

Pyura (Halocynthia) pallida f. formosae: 15.8 mm long syntype included in ZMB 1675. This lot labeled as "Pyura pallida f. formosae Michaelsen, Type!, Takao, Formosa, Sauter" and consisting of 3 then intact inds 13.8–15.8 mm long; only largest one dissected and examined herein. ZMUH T85 (as Pyura momus f. formosae in museum's catalog), coming obviously from same stock as ZMB 1675, should also be syntype(s), but this material is lost.

Halocynthia pallida of Michaelsen (1905): ZMB 841, "Chazalie" Exp., Jamaica, 1 ind. 38 mm long; ZMUH T80, Dar-es-Salaam, east coast of Africa (i.e. Tanzania), Stuhlmann coll., 1 ind. 44 mm long. Michaelsen (1905) redescribed some of the syntypes, collected from Huahine in the Society Isls (probably ZMUH T78), with an illustration (pl. 4, fig. 11), but these are excluded from this species here (for further details, see Appendix herein).

Rhabdocynthia ceylonica: 11.8 mm long syntype, one of 3 syntypes registered as NHML 1907.8.30.9 (labeled as *Herdmania momus* f. ceylonica), collected by Herdman from Ceylon (detailed localities reported in the original description not included on the NHML labels). Two larger specimens lacking mantle bodies; only the smallest (11.8 mm), with gonads, having enough taxonomic information, already examined and described by Monniot and Monniot (1989: 237, fig. 5).

Pyura (Herdmania) ceylonica of Michaelsen (1911): NHUH T147, Alenturai Par, Gulf of Manaar, Ceylon, 1 ind. 20.5 mm long.

Cynthia papietensis: 12 mm long paralectotype (for its designation, see Appendix herein) included in ZMB 3094 (labeled as *H. momus* f. *papietensis*), "Challenger" Exp., Papiete (i.e. Papéeté) Harbor, Tahiti, Society Isls, 10–20 ftms (i.e. 18–36 m), 28 Sept. 1875.

Herdmania momus of Van Name (1952): NHML 1950.2.27.6, "Manihine" Exp., Strait of Zabad, Gulf of Aquaba, on reef at low tide, 11 Feb. 1949, 3 inds 21–26 mm long.

Herdmania momus of Tokioka (1967, part): USNM 11699, exchange from Imperial University of Tokyo (Acc. No. 52210), received 7 Dec. 1910, Kagoshima, Kyushu Is., Japan, E. S. Morse coll., 2 inds 20–25 mm long.

Pyura momus f. typica of Michaelsen (1919): ZMUH T1025 (part), Gimsah Bay, Red Sea, R. Hartmeyer coll., 1902, 1 ind. 23 mm long, another specimen 40 mm long

excluded because of its peculiar features, and another specimen probably of same stock, registered as ZMB 3313, too deteriorated to examine; ZMUH T1053 (part), Jiddah (Djeddah), Red Sea, "Pola" Exp., 1 ind. 22.5 mm long (4 individuals of *H. momus* in this lot excluded; see above).

Pyura momus f. pallida of Hartmeyer and Michaelsen (1928): ZMB 3777, Shark Bay, Western Australia, "Hamburg. SW Australia Exp. 1905", 2 inds 24.0–28.5 mm; excluding ZMUH T1378, 3 inds also collected from Shark Bay during same expedition, because of their unique gonadal features different from those in any known species of this genus (Nishikawa, in preparation).

"Typischen *Pyura pallida*" of Michaelsen (1908): ZMUH T82 (labeled as *Pyura momus pallida* (Heller)), Cienfuegos, Cuba, Captain C. Gagzo coll., 4 inds 29.5–56.0 mm long; ZMUH T83 (*ditto*), Seychelles Isls, Brauer coll., 2 inds 28.5–35.0 mm long; Michaelsen's (1908) remaining material from "Cartagena in Columbien" unavailable.

Herdmania momus of Nishikawa and Tokioka (1975) from shore of Sabiura, Kushimoto-cho, Wakayama Pref., Kii Pen.: NUM-Az0047, Feb. 1973, K. Hayashi coll., 3 inds 29–36 mm long.

Herdmania momus of Nishikawa (1980, part) from Kii Pen.: NUM-Az0048, Hoomon-no-hama, Cape Daio-zaki, Mie Pref., several meters, 25 July 1979, T. Nishikawa coll., 1 ind. 29 mm long, living together with *H. momus*; NUM-Az0049, Suba-no-hama, Cape Daio-zaki, several meters, 25 July 1979, T. Nishikawa coll., 1 ind. 35 mm long; NUM-Az0050, Tagono-ura, near Kushimoto, Wakayama Pref., from undersurface of boulder, intertidal, 27 June 1976, T. Nishikawa coll., 1 ind. 38 mm long; NUM-Az0051, northern beach of Seto Marine Biological Laboratory of Kyoto Univ., Tanabe Bay, Wakayama Pref., several meters, from empty shell of *Megabalanus* sp., 5 Nov. 1975, R. Fukao coll., 1 ind. 29 mm long; NUM-Az0052, Komarujima Island, Tanabe Bay, intertidal, 2 Mar. 1979, T. Nishikawa coll., 2 inds 23.1–24.1 mm long.

Herdmania momus of Nishikawa (1991, part) from Sea of Japan: NUM-Az0053, Ooku, Dogo Is., Oki Isls, Shimane Pref., 3 m, 8 Aug. 1981, T. Nishikawa coll., 1 ind. 15 mm long.

Late Prof. Asajiro Oka's collection of ascidians yet unpublished but having manuscript names: OCUT 5 (M154), "Cynthia satumae", Tanoura, Kagoshima Bay, Kagoshima Pref., 29 Mar. 1896, Mitsukuri coll., 1 ind. 34 mm long; OCUT 26 (M121), "Rhabdocynthia kagosimae", Ushibuka, Amakusa, Kumamoto Pref., T. Aida coll., no collection date, 1 ind. 36 mm long; OCUT 29 (M118), "Rhabdocynthia kagosimae", Enoura, Suruga Bay, Shizuoka Pref., 2–8 Apr. 1904, 4 inds 13–29 mm long; OCUT 30 (M368), "Rhabdocynthia kagosimana", Amami-Oshima Is., Kagoshima Pref., 26 Mar. 1924, K. Tago coll., Imperial Fisheries Institute Collection, 1 ind. 28 mm long; OCUT 38 (M275), "Rhabdocynthia kagosimana", Kagoshima Bay, 10 May 1914, Yamaguchi coll., 4 inds 25–42 mm long; OCUT 98 (M160), "Rhabdocynthia mytiligera", Hyuga (=Miyazaki Pref.), 1896, 2 inds 32–72 mm long; OCUT 335 (M111), "Cynthia satumae", shore of Tanoura, Kagoshima Bay, 29 Mar. 1896, Mitsukuri and Hara coll., 4 inds 35–52 mm long.

New collections: NUM-Az0054, water tank of Shimoda Marine Biological Research Center, Nabeta Bay, Izu Pen., Shizuoka Pref., July 1985, D. Colombera coll., 1 ind. 21 mm long; NUM-Az0055, Nabeta Bay, Izu Pen., 15 Oct. 1993, Y. Hirose coll., 3 inds 35–42 mm long; NUM-Az0056, Nabeta Bay, Izu Pen., subtidal, 10 Dec. 1996, T.

Ishii coll., 6 inds 34–39 mm long; NUM-Az0057, Nabeta Bay, Izu Pen., from buoy, 11 June 1997, T. Nishikawa coll., 4 inds 14–23 mm long; NUM-Az0058, Nabeta Bay, Izu Pen., intertidal, 12 June 1997, T. Nishikawa coll., 1 ind. 26 mm long; NUM-Az0059, from glass slide cultured for 8 months by Mr. H. Yamamoto, fixed on 13 June 1997, 1 ind. 21 mm long; NUM-Az0060, Hatakejima Is., Tanabe Bay, Wakayama Pref., intertidal, 28 Apr. 1998, T. Nishikawa coll., 1 ind. 32.5 mm long; NUM-Az0061, Kagoshima Bay, Kagoshima Pref., Stn 2, Dec. 1984, J. Tsukahara coll., 1 ind. 38 mm long; NUM-Az0062, Kagoshima Bay, Stn 6, Dec. 1984, J. Tsukahara coll., 1 ind. 14 mm long; NUM-Az0063, Kagoshima Bay, Stn 7, Dec. 1984, J. Tsukahara coll., 1 ind. 15.5 mm long; NUM-Az0064, Kin Bay, Okinawa Is., Okinawa Pref., intertidal, 11 Aug. 1999, Y. Hirose coll., 3 inds 22–47 mm long.

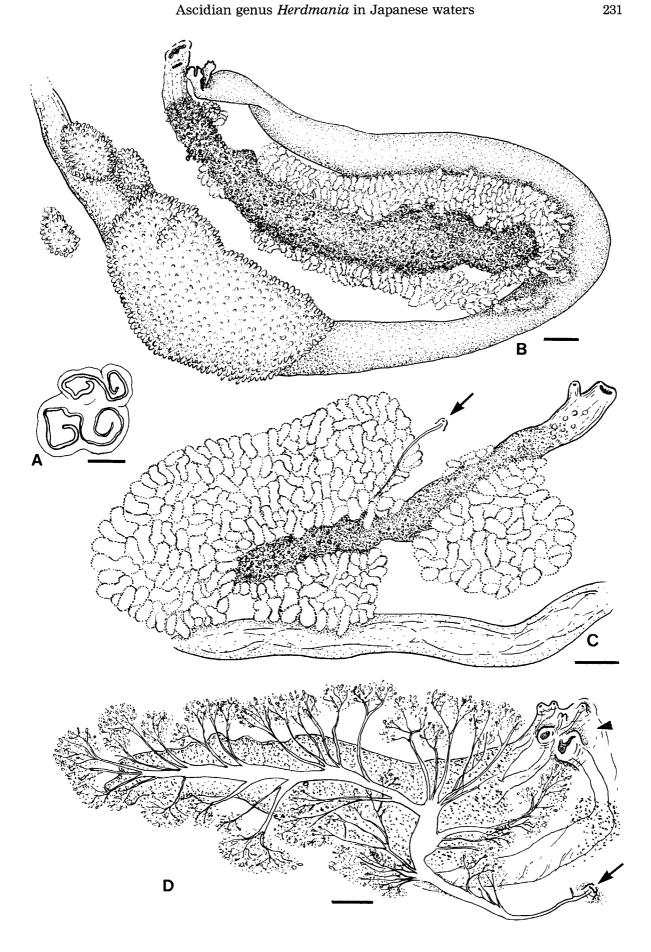
Description. Body roundish and rather robust, up to 56 mm long; smallest mature specimen 15 mm long. Siphons usually indistinct, but sometimes apparent as low prominences. Surface often wrinkled or provided with low protuberances, and covered to various extents with sand grains, bryozoan and didemnid colonies, etc.; *Musculus* bivalves sometimes embedded in tunic. Tunic thin (in smaller specimens) to moderately thick (up to 6 mm in 36 mm long specimen), soft but tough, rarely almost transparent (e.g., in 15.8 mm long syntype of *Pyura pallida* f. *formosae* (ZMB 1675, part)), but usually nearly opaque even in smaller specimens and in lectotype of *Cynthia pallida* (ZMB 704, part), white sometimes with faint tint of brown. Body pale pink in life due to red granules in reticulated tunic vessels (Fig. 2B). Mantle colored deep red only in siphonal area. Density of burred spicules low to moderate in tunic, mantle, and visceral tissues, although variable among individuals.

Tentacles of several sizes, about 24 in number, well developed and branched in 3 orders. Branchial folds usually consisting of 8 complete folds and ventral-most incomplete fold (latter discernible only anteriorly) on each side, but often only 8 (all complete) on left; in 31 mm long lectotype of *C. pallida* (ZMB 704, part), 10 folds (all complete) present on left, but folds uncountable on right due to injury; in syntype of *P. pallida* f. *formosae*, 7 complete folds on left, 7 complete and 1 incomplete folds on right. Ciliated groove simple C-shaped and open anteriorly, with both horns inrolled in larger specimens; exceptionally, in 72 mm long specimen of OCUT 98 (M160), groove consisting of 2 inverted-S-shaped pieces (Fig. 5A). Dorsal languets distinct. Atrial velum usually divided into many membranous projections, but rarely represented by low, simple crest instead; no atrial tentacles. Stomach covered densely with hepatic lobules. Intestinal loop very wide. Anal margin smooth or slightly or deeply bi- or 4-lobed (Fig. 5B).

One gonad on each side; left one in intestinal loop along intestine's dorsal branch (Fig. 5B). Each gonad large, elongated; left and right ones similar to each

Fig. 5. *Herdmania pallida* (Heller). A, complicated ciliated groove of 72 mm long specimen from Miyazaki Pref. (OCUT 98 (M160)); B, alimentary canal and gonad of lectotype from Mauritius (ZMB 704, part); C, right gonad and heart of 29 mm long specimen from Daio-zaki (NUM-Az0048), Kii Peninsula, showing supernumerary aperture of testis (arrow); D, right gonad (spent) of 36 mm long specimen from Kushimoto-cho, Kii Peninsula (NUM-Az0047), showing abnormally positioned aperture of vas deferens (arrow) and multiple orifices of oviduct (arrowhead). Scales 1 mm.

Ascidian genus *Herdmania* in Japanese waters



other in structure. However, 29 mm long specimen from Daio-zaki and 36 mm long specimen from Sabiura, Kii Peninsula, each with aberrant right gonad: former with supernumerary aperture of isolated sperm duct (Fig. 5C); latter with aperture of vas deferens located apart from cluster of 6 apertures of oviduct (Fig. 5D). Ovary usually fringed (and often somewhat covered) with testicular follicles along almost its whole contour (e.g., in lectotype of C. pallida: Fig. 5B); exceptionally, in syntype of P. pallida f. formosae from Taiwan, ovary surface covered with testicular follicles except for narrow axial zone. Vas deferens opening through single aperture close to oviduct orifice; male aperture sometimes sessile, as in lectotypes of C. pallida and P. momus f. kyamanensis, but often located on top of very low papilla. No additional ducts nor apertures of testicular follicles present. Very rarely, margin of aperture of vas deferens provided with pair of fine papillae opposite to each other (in 44 mm long specimen from Dar-es-Salaam, ZMUH T80), or mesial half of margin forming blunt triangular projection (in syntype of P. pallida f. formosae). No membranous organ or any other organs around orifice end of oviduct; instead, minute papilla or ridge rarely detectable between apertures of oviduct and vas deferens (in syntype of *P. pallida* f. *formosae*).

Remarks. The specimens described by Das (1936), Monniot (1965, 1983), and Monniot and Monniot (1987) as *Pyura momus* or *H. momus*, together with those by Monniot (2002) as *H. pallida* (see "Confirmed previous records" above for details) are here regarded as conspecific with *H. pallida* only on the basis of the clear figures provided by these authors. The pinkish body of *H. pallida* in life (see Fig. 2B) is highly reminiscent of fig. 2 of the colored pl. 1 of the original description of *Cynthia momus* by Savigny (1816); perhaps the figured specimen had an opaque tunic. If so, the figure may portray a specimen of *H. pallida*. This suggestion, however, is belied by the above-stated definition of *H. momus* as usually having a very thin and almost transparent tunic, through which the reddish mantle body is visible; furthermore, *H. pallida* has no membranous accessaries around the orifice of the oviduct, contrary to the original description of *H. momus*. As shown in the present study, the Gulf of Suez is inhabited by both *H. momus* and *H. pallida*.

Confirmed distribution. Japanese waters, intertidal to several meters: Oki Isls, Shimoda (Sagami Bay), Kii Pen., Kagoshima Bay, and Okinawa Is. Pacific, down to 70 m: Taiwan (=Formosa), Vietnam, Java Sea, Guam, Palau, Tahiti and Moorea of the Society Isls, New Caledonia, and Hawaii. Indian Ocean: Shark Bay (W. Australia), Sri Lanka (=Ceylon), Red Sea (including Gulf of Suez), Djibouti, Zanzibar and Dar-es-Salaam (East African coast), Mozambique, Seychelles, and Mauritius. Atlantic: Panama, Cuba, Antilles, and Brazil.

Herdmania japonica (Hartmeyer, 1909), comb. nov. (Figs 6–7)

Puyra pallida f. japonica Hartmeyer, 1909: 1340 (established by bibliographical reference to the "japanisches Form" of Halocynthia pallida described by Hartmeyer (1906); see below).

Probable synonym

Rhabdocynthia siphonalis Oka, 1933: 648–650, text-figs A–B (name-bearing type not yet examined).

Confirmed previous records

Halocynthia pallida: Hartmeyer 1906: 4, text-fig. 2. [Nec Heller, 1878]
Herdmania momus: Tokioka 1953: 277–281, pl. 3, fig. 7, pl. 68, figs 3–6, pl. 69, figs 1–5 (figs 5–6 of pl. 3 excluded); Nishikawa 1991: 137 (partim). [Nec Savigny, 1816]
Herdmania momus f. siphonalis: Tokioka 1953: 281–282, pl. 69, fig. 6, pl. 70, figs 1–6. [Nec Oka, 1933]

Specimens examined. *Pyura pallida* f. *japonica*: part of syntype lot from Tokyo Bay, Japan, 600 m, collected by F. Doflein (Mus. München), ZMB 2802, 2 inds 42–56 mm long. Although the type series consisted of "11 Exemplare" (Hartmeyer

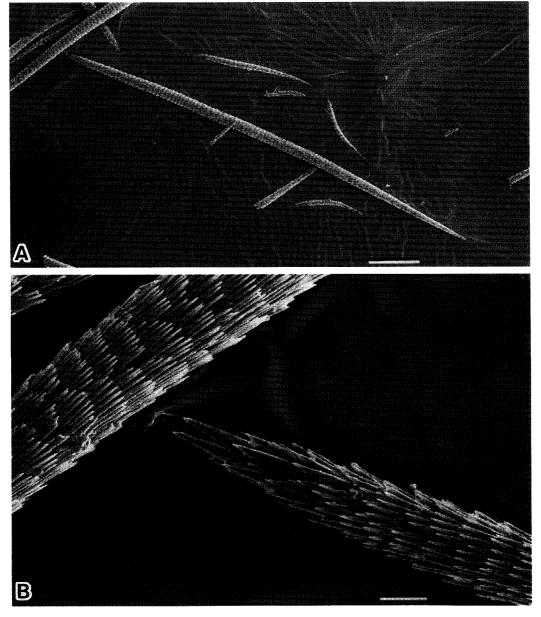


Fig. 6. SEM images of spicules of a specimen of *Herdmania japonica* (Hartmeyer) from Oki Isls (Stn. 1; NUM-Az0068). A, spicules showing length variation; B, enlargement of part of A, showing burred surface. Scale $100 \, \mu \text{m}$ for A, $10 \, \mu \text{m}$ for B.

1906: 4), only these two syntypes are now available.

Herdmania momus of Tokioka (1953) from eastern part of Sagami Bay, Japan: NSMT-PcR 84 (=Tokioka's (1953) #194), South Amadaiba in Amadaiba, 500 m, 21 Aug. 1935, 2 inds 75–82 mm long; NSMT-PcR 171 (= #78), South Amadaiba in Amadaiba, 400 m, 17 Jan. 1937, 1 ind. 42 mm long; NSMT-PcR 199 (#104), Hasaki off Sasima, 16 m, 31 July 1939, 1 ind. 52 mm long; NSMT-PcR 256 (#153), off Araibama, Misaki, 27 m, 11 June 1951, 1 ind. 120 mm long.

Herdmania momus f. *siphonalis* of Tokioka (1953) from eastern part of Sagami Bay: NSMT-PcR 181 (= #87), off Jyogashima, 60 ftms (i.e. 109 m), 4 Aug. 1936, 45 mm long body with elongated siphons; NSMT-PcR 64b (= #187), Amadaiba, 50 ftms (i.e. 91 m), 3 Aug. 1934 (as "1933" in Tokioka (1953: 282)), 65 mm long body with elongated siphons.

Herdmania momus of Nishikawa (1991) from Sea of Japan: NUM-Az0065, off Noto-ogi, Noto Pen., Ishikawa Pref., 15–40 m, 9 June 1975, T. Shinya coll., 1 ind. 88 mm long; NUM-Az0066, off Uchiura Bay of Wakasa Bay, Fukui Pref., 40 m, 11 June 1980, T. Yasuda coll., 3 inds 19.0–40.5 mm long; NUM-Az0067, from rope set in front of Noto Marine Biological Station, Tsukumo Bay, Ishikawa Pref., very shallow, 10 May 1981, H. Michibata coll., 1 ind. 38 mm long; NUM-Az0068, Oki Isls, Shimane Pref., stn 1, 36°10.20′N, 133°13′E, 47–55 m, 9 Sept. 1985, H. Saito and T. Nishikawa coll., 3 inds 35–45 mm long; NUM-Az0069, Oki Isls, stn 2, 36°10.20′N, 133°14′–15′E, 40–55 m, 10 Sept. 1985, H. Saito and T. Nishikawa coll., 2 inds 32–40 mm long; NUM-Az0070, Oki Isls, stn 5, 36°10.29′N, 133°13.52′E, 35–45 m, 12 Sept. 1985, H. Saito and T. Nishikawa coll., 2 inds 20–44 mm long, living together with H. momus.

Late Prof. Asajiro Oka's collection of ascidians, unpublished but with manuscript names: OCUT 66 (M159), "Rhabdocynthia elliptica", no collecting data, 8 inds 47–60 mm long; OCUT 81 (M125), "Rhabdocynthia elliptica", 35°6.20′N, 139°31.30′E, 400 ftms (i.e. 728 m), 9 Aug. 1903, A. Owston coll., by his research yacht "Golden Hind", 2 inds 55–65 mm long.

New collections: NUM-Az0071, off west coast of Satsuma Pen., Kyushu Is., 31°26′N, 129°52′E, 300–320 m, 15 Nov. 1977, T. Imaoka coll., 1 ind. 52 mm long; NUM-Az0072, Tsukumo Bay, Ishikawa Pref., 20 m, 28 July 1992, T. Nishikawa coll., 1 ind. 130 mm long; NUM-Az0073, Enshu-nada Sound off Aichi Pref., 50–150 m, 3 Mar. 1993, M. Kashihara coll., 1 ind. 63 mm long; NUM-Az0074, probably Enshu-nada Sound (or Ise Bay) off Aichi Pref., depth unknown, Mar. 1993, M. Kashihara coll., 1 ind. 112 mm long; NUM-Az0075, north offshore of Ikata-cho, Ehime Pref., Seto Inland Sea, 15.1 m, 27 May 1996, M. Ootani coll., 1 ind. 115 mm long, living together with *H. momus*.

Description. Body nearly globular or flattened laterally. Up to 130 mm long; smallest mature individual 32 mm long. Siphons usually indistinct. Surface often wrinkled and/or provided with low protuberances and covered partly with sand grains, shell debris, and hydroid, bryozoan, or ascidian colonies; *Musculus* bivalves rarely embedded in tunic. Tunic thin (about 1.0–1.5 mm thick in smaller specimens and those from deep waters) to moderately thick (up to 12 mm in 130 mm long specimen from 20 m deep), soft but tough, rarely semi-transparent but usually almost opaque even in specimens with thin tunic, colored white superficially, with faint to dark tint of brown; many fine, root-like processes on wide ventral area entrapping fine sand grains, replaced by few stout processes in larger specimens inhabiting shallow, hard substrata. Tunic impregnated with fragments of burred

spicules to various degrees in different individuals. In life, 130 mm long individual from Tsukumo Bay (NUM-Az0072) with tunic colored orange to pink and showing many fine, white, longitudinal lines on pinkish background inside siphons. Density of burred spicules (Fig. 6) more or less high in mantle and visceral tissues; their dense impregnation sometimes resulting in high fragility of mantle.

Tentacles of several sizes, about 24 (rarely up to 50) in number, well developed and branched in 3 (very rarely 2 or 4) orders; exceptinally, 130 mm long specimen from Tsukumo Bay with only 18 tentacles branched in 1 order. Branchial sac with 10 (or very rarely 9) to 11 (or 12) complete folds, often with additional ventral-most incomplete fold anteriorly on each side; in largest specimen (130 mm long) from Tsukumo Bay, 10 folds on left and 11 on right without any incomplete ones, while in the smallest one (19 mm) from Wakasa Bay, 10 complete folds +1 incomplete one on left and 11+0 folds on right; in 36 mm long specimen from Oki Isls, only 9+0

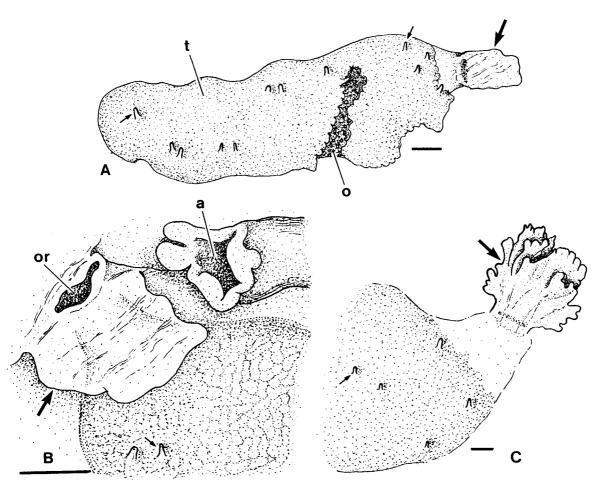


Fig. 7. Herdmania japonica (Hartmeyer), showing variation in flap (large arrow) issuing from mesial lip of oviduct orifice and also showing testicular follicles (t) over nearly whole of mesial surface of gonad, with several ejectors (small arrows). A, right gonad of 56 mm long syntype from Tokyo Bay (ZMB 2802), with part of ovary (o) visible; B, anus (a) and orifice end of left gonad of 45 mm long specimen from Oki Isls (NUM-Az0068), its transversely elongated oviduct orifice (or) clearly visible; C, orifice end of right gonad of 130 mm long specimen from Tsukumo Bay (NUM-Az0072), showing fan-shaped flap somewhat folded and toothed-margined. Scales 1 mm.

folds on each side. Ciliated groove simple C-shaped and opening anteriorly in smaller specimens from shallow waters and all deep specimens, but groove more or less undulating with both horns inrolled up to 3 times (often cut into pieces) in larger specimens from shallow waters. Dorsal languets distinct. Atrial velum divided into many membranous projections; no atrial tentacles. Stomach covered densely with hepatic lobules. Intestinal loop very wide. Anal margin divided into 2 to 12 distinct lobules.

Single gonad on each side; left one in intestinal loop along intestine's dorsal branch. Each gonad large, elongated; left and right ones similar to each other in structure. Ovary usually tubular with mesial surface covered almost completely with testicular follicles (Fig. 7A), but follicles sometimes invading into patches of attachment surface of ovary while leaving wide area of mesial surface uncovered; exceptionally, in 112 mm long specimen probably from Enshu-nada (NUM-Az0074), immature testis enclosed by mature ovary. Testis markedly sinuate over mesial surface of ovary only in one specimen (NSMT PcR 181). Testis opening exclusively through some to many minute, erect ejectors over gonadal surface.

Oviduct orifice completely or almost sessile and elongated transversely, membranous flap issuing from its mesial lip into peribranchial cavity. Flap usually thin and extensive, rarely thick and inconspicuous, simple rectangular in smaller specimens and those from deep waters (Fig. 7A, B), but wide and fan-shaped with complicated margin in some larger specimens from shallow waters (Fig. 7C).

Remarks. Rhabdocynthia siphonalis was established by Oka (1933) for an ascidian with a very long atrial siphon, collected from south of Misaki, Sagami Bay, at depths of 150–250 m. It seems probably to be a junior synonym of *H. japonica*, judging from my examination of Tokioka's (1953) specimens of *H. momus* f. siphonalis with similar external appearance and dredged from nearly the same region as Oka's. Unfortunately, the name-bearing types of *R. siphonalis* Oka are now lost.

My reexamination of the holotype of *Herdmania momus* var. *curvata* Kott, 1952 (=*H. curvata* Kott on the museum label) (AMS Y1811), about 30 mm long with a 35 mm long posterior extension of the tunic, from Queensland, Australia, revealed a close relationship with *H. japonica*. Contrary to the original description (Kott 1952: 282–283, fig. 129), a fan-shaped and rather thick membrane issues from the mesial lip of the orifice of the sessile oviduct in each gonad, and the sinuous testis is covered over its whole surface with many minute and sessile (hence nearly undetectable) ejectors. These two features were also detected by my reexamination of the about 25 mm long holotype of *H. contorta* Monniot, 1992 (MNHM S2HER1) from New Caledonia (Monniot 1992: 18–19, figs 6B, 7), although the membrane is much less developed in *H. contorta* than in the holotype of *H. curvata*. Therefore, these two species are safely treated as synonyms, with *H. curvata* being the senior and valid name. Although it is obvious that *H. curvata* is closely related to *H. japonica*, I am now reluctant to synonymize *H. curvata* with the latter, because the sinuate arrangement of testis is very rare and the ejectors are usually erect in *H. japonica*.

Herdmania momus of Tokioka (1967: 205–206, part) from off Cape Manazuru, Sagami Bay, Japan ("Albatross" Stn 3698, 5 May 1900, 153 ftms (i.e. 279 m) deep) and registered as USNM 11780, may possibly be referable to *H. japonica*, although a detailed examination was impossible. My observation of eight individuals sent from the National Museum of Natural History, Smithsonian Institution, showed much

deterioration of the mantle bodies; in a $56 \, \text{mm}$ long specimen a fragmental gonad was detected, which was furnished with a peculiar membranous flap. However, exact identification could not be confirmed, and this record was excluded from those of H. japonica in the present study.

Confirmed distribution. Japanese waters: Tokyo Bay, 600 m; eastern part of Sagami Bay, 16–720 m; Enshu-nada Sound, depth unknown; Seto Inland Sea, 15.1 m; east coast of Noto Pen., to 40 m; Wakasa Bay, 40 m; Oki Isls, 35–55 m; off western coast of Satsuma Pen., Kyushu Is., 300–330 m.

Herdmania mauritiana (Drasche, 1884), comb. nov. (Fig. 8)

Cynthia mauritiana Drasche, 1884: 374, pl. 4, figs 1-3.

Herdmania insolita Monniot and Monniot, 2001: 339–341, text-figs 102–103 (based only on literature). [Syn. nov.]

Confirmed previous record

Rhabdocynthia tenuis (?): Sluiter 1895: 184–185, pl. 10, figs 10–12. [Nec Herdman, 1891]

Specimens examined. *Cynthia mauritiana*: holotype, NHMW Mollusca 100832, consisting of 26 mm long body without mantle body attached to black glass plate, and mantle body deprived of tunic, collected from "Ins. Mauritius" (i.e. Mauritius Is.); these two body parts are judged to belong to the same individual, because of their general similarity in shape and their relative size.

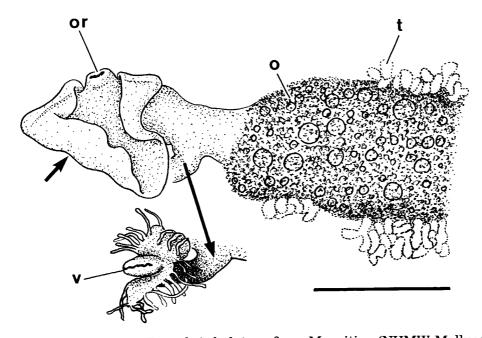


Fig. 8. *Herdmania mauritiana* (Drasche), holotype from Mauritius (NHMW Mollusca 100832). Orifice end of left gonad, showing hood (arrow) around oviduct orifice (or), aperture of vas deferens (v) surrounded by filament-bearing membrane, ovary (o), and testicular follicles (t). Scale 1 mm.

Rhabdocynthia tenuis (?) of Sluiter (1895) from Ambon, Banda Sea, Indonesia: ZMA TU 896, 1 ind. 25 mm long, collected by R. Semon.

New collections from Japanese subtropical waters in Okinawa Pref.: NUM-Az0076, Kabira Bay, Ishigaki Is., intertidal, 24 June 1975, T. Nishikawa coll., 1 ind. 13 mm long; NUM-Az0077, shore in front of Univ. Ryukyus Tropical Biosphere Research Center Sesoko Laboratory, Sesoko Is., 1 Jan. 1976, K. Yamazato coll., 1 ind. 20 mm long.

Description. Tunic very thin (in holotype) or moderately thick (up to 3 mm in 20 mm long specimen), soft but tough, semi-transparent and white, containing fragments of burred spicules rather densely in holotype but very sparsely in other specimens from Japan and Ambon. Tunic surface bearing pieces of Halimeda-like calcareous green algae in holotype.

Burred spicules included in mantle and viscera rather densely (in holotype) or sparsely (in others). Tentacles 24 (in 13 mm and 25 mm long specimens) to 30 (in 20 mm one), larger and smaller tentacles alternating regularly, branched in 2 orders. Number of tentacles and branchial folds in holotype unmeasured due to heavy injury. Ciliated groove C-shaped and opening anteriorly. Dorsal languets distinct. Atrial velum unclear, without tentacles. Seven complete (+1 incomplete) branchial folds on left and 8 on right in 20 mm long specimen, 7+1 folds on each side in 2 mm long specimen, and 7 folds on each side in 13 mm one. First intestinal loop wide and open. Anus bilobed with smooth edges.

Single elongated gonad on each side, left one in intestinal loop; consisting of central ovary fringed almost wholly (though never covered) with testicular follicles. In each mature gonad in holotype and 20 and 25 mm long specimens, terminal free part of oviduct very short and accompanied mesially by large, rectangular hood surrounding half or less of free part of oviduct (Fig. 8); vas deferens opening as elongated slit at end of short, erect duct close to oviduct and hood. No additional ducts nor apertures of testicular follicles present. End of vas deferens furnished on each side with membranous ridge fringed with 12 or more (up to 36 in 25 mm long specimen) filamentous projections (Fig. 8). In 13 mm long specimen with immature ovary and nearly mature testis, hood less developed and filamentous projections few and indistinct.

Remarks. The Naturhistorisches Museum Wien keeps the ascidian and echiuran specimens, including the name-bearing types, described by Dr. Richard von Drasche: NHMW Mollusca 100832, collected from "Ins. Mauritius", is the only specimen kept under the name of *Cynthia mauritiana*. Although not marked as such, this specimen is evidently its holotype. It is quite similar to the original description and illustration of this species established for "Ein Exemplar" from "Insel Mauritius", especially in the shape and size of the body, in some "Steinalgen" slightly covering the surface, the "weissen kleinen Nadeln" (white small needles) in the mantle, and the gonads consisted of an axial, elongated ovary and a peripheral testis.

The holotype of *Cynthia mauritiana* is also quite in accord with the original description of *Herdmania insolita* in its significant features, especially the elongate ovary fringed with the testis along with the oviduct flange and filament-born ridges around the aperture of the vas deferens. In *H. insolita*, eight branchial folds were recorded on each side. Although heavy injury of the branchial sac made it impossible to count the number of folds in the holotype of *H. mauritiana*, its origi-

nal description says "Der Kiemensack hat jederseits acht Falten." There seem, therefore, to be no taxonomically significant differences between these two species, and *H. insolita* is safely regarded as a junior synonym of *Cynthia mauritiana*. The recently established name *H. insolita* cannot be treated as a *nomen protectum* under the Article 23.9 of the present International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 2000).

Distribution. Sesoko Is. and Ishigaki Is., Ryukyu Isls, SW Japan, intertidal; Yap Is., Federated States of Micronesia, 7m; Palau (Belau), Micronesia, 1m; Ambon, Indonesia; Mauritius Is., Indian Ocean.

Herdmania subpallida sp. nov.

(Fig. 9)

Confirmed previous record

Herdmania momus: Nishikawa and Tokioka 1976: 400 (partim). [Nec Savigny, 1816]

Type material. *Holotype*: NUM-Az0078, specimen 23 mm $long \times 27$ mm wide, collected by S. Ooishi at Honohoshi, Amami-Oshima Is., Kagoshima Pref., 11 July 1963; described as *H. momus* by Nishikawa and Tokioka (1976), together with two specimens from Seso, Amami-Oshima, which are now lost.

Description. Body roundish, flattened laterally (Fig. 9A). Both siphons present but unremarkable; branchial siphon situated terminally and atrial one nearly in middle of body. Surface weakly wrinkled and partly covered with fine filaments probably of protistan genus *Zoothamnium* sp. Tunic up to 2mm thick, soft but tough, white and nearly opaque. Burred spicules very sparse in tunic, mantle, and viscera; isolation efforts for SEM observation unsuccessful.

Mantle musculature as network of thin bundles issuing from both siphons and covering nearly dorsal half of body. Tentacles of several sizes, about two dozen in number, well developed, branched in 3 orders. Ciliated groove C-shaped and open anteriorly. Dorsal languets distinct. Atrial velum unclear, lacking tentacles. Number of branchial folds 9 on left and 8 on right, with following formula: L. D. 2 (12) 2 (17) 2 (15) 2 (15) 2 (15) 2 (18) 1 (16) 1 (12) 1 (7) 0 V; R. D. 2 (11) 3 (17) 2 (14) 2 (14) 2 (13) 1 (14) 1 (10) 1 (6) 0 V. Hepatic gland composed of 4 lobes made of multiple round papillae (Fig. 9B). First intestinal loop wide and open. Anal margin smooth.

Single, fully mature, oval gonad on each side, left one occupying first intestinal loop; central ovary fringed and partly covered with testicular follicles (Fig. 9B, E). Oviduct sessile with large slit; flap issuing from mesial lip of slit, rectangular and thin (on left) or rounded and somewhat thickened (Fig. 9C–D). Vas deferens opening at posterior mesial (=anti-oviduct) base of left flap, but at nearly middle of anterior mesial margin of right flap (Fig. 9C–D). No additional ducts nor apertures of testicular follicles present.

Remarks. The present specimen from Amami-Oshima Island is similar to *H. pallida* in the arrangement of the ovaries and testes, but clearly distinguishable from the latter by the presence of an accessary flap issuing from the mesial lip of the sessile oviduct. Among the species with such accessary flaps or hoods around the oviduct orifices, the manner of opening of the testis in this specimen is obviously unique. The specific name for this new species comes from *sub* (from Latin,

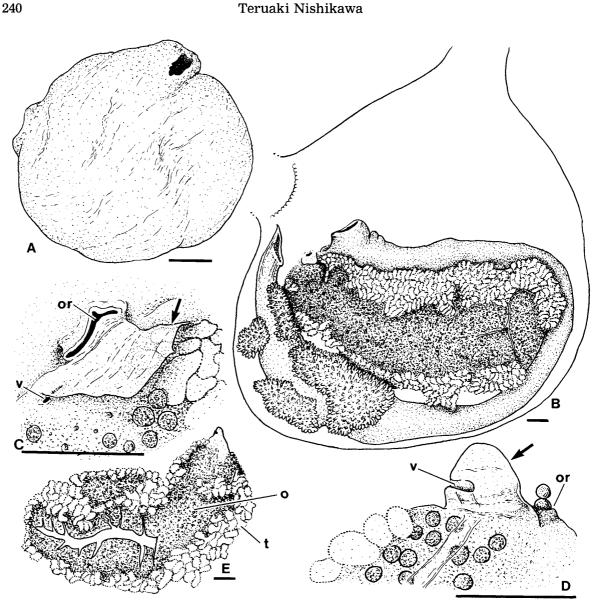


Fig. 9. *Herdmania subpallida* sp. nov., holotype from Amami-Oshima Island (NUM-Az0078). A, body, side view; B, inner left side of mantle body; C, D, orifice ends of left and right gonads, respectively, showing flap (arrow) issuing from mesial lip of oviduct orifice (or) and aperture of vas deferens (v); E, right gonad, proximal half of vas deferens missing, showing ovary (o) fringed with testicular follicles (t). Scales 5 mm for A, 1 mm for B–E.

meaning "somewhat")+pallida.

Distribution. Amami-Oshima Island, SW Japan.

Herdmania kiiensis sp. nov. (Figs 10–11)

Confirmed previous record

Herdmania momus: Nishikawa 1980, table 1 (partim). [Nec Savigny, 1816]

Ascidian genus *Herdmania* in Japanese waters

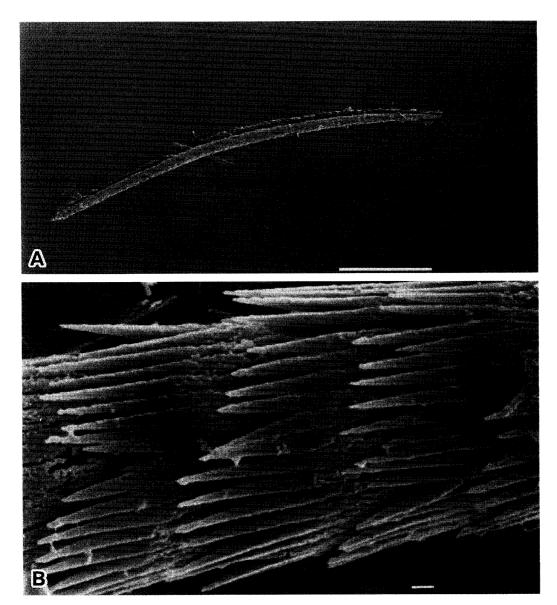


Fig. 10. SEM images of spicules of *Herdmania kiiensis* sp. nov., holotype from Kii Peninsula (NUM-Az0079). A, a spicule; B, magnification of part of A, showing burred surface. Scale $100 \, \mu \mathrm{m}$ for A, $1 \, \mu \mathrm{m}$ for B.

Type material. *Holotype*: NUM-Az0079, specimen 31 mm $\log \times 26$ mm wide, collected by T. Nishikawa at Shinden, Nigijima-cho, Mie Pref., east coast of Kii Pen., several meters deep, 29 July 1979, living together with 23 mm long individual of *H. momus* (NUM-Az0010, see section on *H. momus* above); reported as *H. momus* by Nishikawa (1980).

Description. Body roundish, flattened laterally (Fig. 11A). Both siphons distinct; branchial siphon terminal and atrial one subterminal. Surface somewhat wrinkled, covered sparsely with shell debris and small ascidian (didemnid and botryllid) colonies. Test thin, up to 1 mm, but tough, pale brownish, semitransparent to opaque. Burred spicules (Fig. 10) found sparsely in tunic, but densely in mantle and viscera.

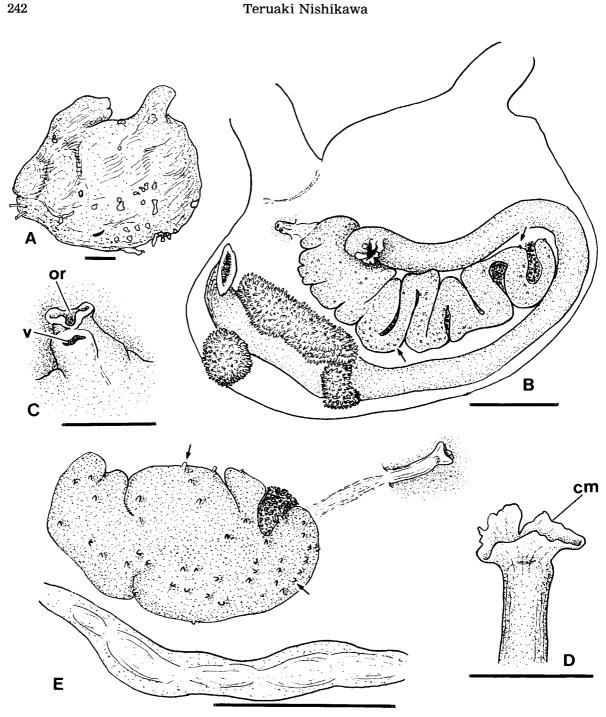


Fig. 11. *Herdmania kiiensis* sp. nov., holotype from Kii Peninsula (NUM-Az0079). A, body, side view; B, inner left side of mantle body, with erect ejectors (arrows) over left gonad; C, D, magnified view of orifice ends of oviducts of left and right gonad, respectively, showing oviduct orifice (or), aperture probably of vas deferens (v), and cone-shaped membrane surrounding oviduct orifice (cm); E, right gonad and heart, with erect ejectors (arrows) over gonad. Scales 5 mm for A, B, E, 1 mm for C, D.

Mantle musculature as network of thick bundles issuing from both siphons and covering nearly dorsal half of body. Tentacles of several sizes, 24 in number, and branched in 2 orders. Ciliated groove C-shaped and open anteriorly. Dorsal languets distinct. Atrial velum unclear, without tentacles. Eight complete and 1 incomplete (discernible only anteriorly) branchial folds on left and 9 complete and 1 very rudimentary folds on right, with formula: L. D. 2 (11) 2 (16) 2 (20) 2 (22) 4 (20) 4 (21) 3 (17) 3 (18) 1 (6) 0 V; R. D. 2 (6) 2 (13) 3 (21) 4 (22) 3 (19) 2 (14) 2 (13) 2 (12) 1 (10) 0 (1) 0 V. Hepatic gland composed of 2 lobes made of multiple round papillae (Fig. 11B). First intestinal loop wide and open. Anus opening on somewhat twisted endpart of rectum; anal margin cut irregularly into several lobules.

Single, fully matured, oval gonad on each side; left one situated in intestinal loop. Elongated ovary almost completely covered with testis; sinuate arrangement of latter being obvious only on left (Fig. 11B–C). On left, orifice of oviduct opening at tip of short, free tube, with sessile aperture probably of vas deferens nearby (Fig. 11B); on right, oviduct orifice situated at tip of elongated, free tube, accompanied by cone-shaped surrounding membrane (Fig. 10D) but without any other apertures nearby. Mesial surface of testicular follicles provided densely with fine and short but erect ejectors on both right and left sides (Fig. 11B–C).

Remarks. The present specimen from the Kii Peninsula is similar to H. momus, H. japonica, and H. curvata (=H. contorta) in the presence of an often sinuately arranged testis covering the ovary, and numerous ejectors over the testis; however, the specimen is easily distinguishable from all these species by the complete lack of hoods and flaps associated with the end of the oviduct. Instead, the cone-shaped membrane surrounding the oviduct orifice of the right gonad seems to be unique among all the known species of Herdmania.

The sinuate testis arrangement seen in *H. kiiensis* is reminiscent of the sinuous gonad on each side reported in the original description of *Herdmania inflata* (Van Name, 1918) (Van Name 1918: 74–76, text-figs 12–18) [for the transfer of *Pyura inflata* Van Name, 1918 to this genus see Monniot (1992)]. My reexamination of the holotype of the latter species (USNM 6037), which was collected from Sulu Archipelago at a depth of 97 ftms (i.e. 177 m) confirmed the existence (though detectable only sparsely) of burred spicules and a sinuous testis overlying the partly mature and roughly tubular ovary. The orifice of the oviduct is not accompanied by any membranous hood nor flap. The testis is furnished with many fine but erect ejectors over its mesial surface, and there is no aperture of the vas deferens near the oviduct orifice. *Herdmania inflata* may be related to *H. kiiensis*, but it is clearly distinguishable from the latter in the stalk-like anterior projection of the body and in the details of how the ovary and testis open.

The absence of a flap or hood around the oviduct orifice and the occurrence of ejectors in *H. kiiensis* is reminiscent of *H. pennata* Monniot and Monniot, 1991 from New Caledonia and vicinity (Monniot and Monniot 1991: 412–413); however, the ejectors in the latter species are confined to the axial part of the gonad, issuing from the vas deferens. Furthermore, *H. pennata* has the ovary fringed, not covered, with testicular follicles. These two species are doubtlessly different from each other.

Distribution. Nigijima-cho, Mie Prefecture, east coast of the Kii Peninsula, Japan, several meters.

Herdmania sp.

Confirmed previous record

Herdmania momus: Millar 1975: 317–318, text-fig. 94 (partim). [Nec Savigny, 1816]

Specimen examined. One 42 mm long specimen, S of Goto Isls, Kagoshima Pref., Kyushu, Japan, 32°21′N, 128°39′E, 274–366 m, 4 Mar. 1933, deposited at ZMK without registration number.

Description. Body roundish, flattened laterally. Tunic very thin like paper, semitransparent to translucent, white. Fragments of burred spicules found densely in tunic; such spicules also embedded densely in mantle and viscera.

Tentacles of several sizes, about 20 in number, branched in 3 orders. Ciliated groove C-shaped and open anteriorly with both horns curled to right (as shown in Millar 1975, text-fig. 94e). Dorsal languets distinct. Atrial velum unclear, without tentacles. Branchial folds 13 (?) complete+1 incomplete (latter discernible only anteriorly) on left and 15+1 on right. First intestinal loop wide and open. Anal margin cut into 6 lobules.

Single, elongated, and completely empty gonad on each side; left one situated in intestinal loop; location of gonads suggested by dense accumulation of fragmented spicules much finer than spicules elsewhere. Many ejectors over gonadal surface. Oviduct sessile with large slit; on right, small flap issuing from slit's mesial lip; flap present but much smaller on left. Large, flattened space discernible probably between peribranchial epithelium and epidermis (and visceral wall) on left, occupying bottom half of 1st intestinal loop and ventral half of intestine, as shown in Millar (1975, text-fig. 94i), with anti-orifice (=anterior) one-fourth of gonad underlain by space. Similar space also found on right, with anti-orifice half of gonad underlain by space. Nemertean worm found in peribranchial cavity.

Remarks. This deep-water specimen from off Kyushu is similar to *H. japonica* especially in the occurrence of many ejectors over the gonadal surface and a membranous flap issuing from the oviduct orifice; however, this specimen seems unique in having a large flattened space on each side and in the large number (up to *ca.* 15 on each side) of branchial folds for a medium-sized (42 mm long) body. The space was regarded as a "large spent gonad" by Millar (1975). Its real nature remains unclear to me, but perhaps it results from the presence of the symbiotic nemertean. Complete emptiness of the gonads also prevents further taxonomic precision. Additional material from this locality is desirable.

Distribution. South of Goto Isls, Kyushu, Japan, 274–366 m deep.

Discussion

Evaluation of diagnostic characters

Although tunic thickness usually changes with growth, the invariable occurrence of a thin tunic in *H. momus* even in larger specimens should be noted here. The shape and fine structure of the burred spicules seem very stable among the species studied here, while their size and density seem variable among individuals; therefore, no characters of the spicules were used for specific distinction in the present study. The number of branchial folds also seems correlated positively with

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Ascidian genus *Herdmania* in Japanese waters

Table 2. Comparison of Japanese (marked with single asterisk *) and some other species of the genus *Herdmania* with a single massive gonad on each side, referred to in the present paper.

Species	Oviduct orifice accompanied by**	Testis opening through many ejectors over gonad	Testis situated over (O) or fringing (F) ovary
*H. momus	rounded hood	Yes	0
*H. pallida	nothing	No	${f F}$
*H. japonica /H. curvata	rectangular or fan-shaped flap	Yes	O
*H. mauritiana	rectangular hood	No	${f F}$
*H. subpallida	rectangular rounded flap	No	F
*H. kiiensis /H. inflata	nothing***	Yes	O
*Herdmania sp.****	rectangular flap	Yes	unknown
H. polyducta	spade-shaped flap	Yes	${f F}$
H. pennata	nothing	Yes****	${f F}$

^{**} For distinction between "hood" and "flap", see text.

body size, as was mentioned in the section concerning *H. momus*, and therefore it is of little taxonomic significance. *Herdmania* sp. with 15 folds in a 42 mm long specimen perhaps represents an exception; that number seems large for its size. Lobation of the anal margin may be variable and seems of limited diagnostic significance; however, there is a marked tendency for the anal margin to be smooth in *H. pallida* and *H. subpallida*, cut into many distinct lobules in *H. monus*, and moderately lobulated in the remaining Japanese species.

Instead of the characters just mentioned, I have adopted gonadal features for specific delimitation in this genus. These characters are the relative position of the testis and ovary, the nature of the testis openings (many ejectors vs. a single aperture of the vas deferens), the presence or absence of a membranous organ near the oviduct orifice, and, if present, its general form (distinguished as "hood"- or "flap"-like; for further details see the sections on *H. momus* and *H. japonica*) and the shape of the margin. The mentioned characters except the last one seem well-used among ascidian taxonomists.

Sympatric occurrences

Herdmania momus and H. japonica were found attached firmly to each other at Ikata-cho, Ehime Pref., Seto Inland Sea, Japan. This represents true sympatry in the strictest sense. The robustness of the morphological gap between the two kinds of membranous organ around the oviduct orifice ("hood" in the former species and "flap" in the latter) as a taxonomic criterion at the species level may be corroborated by this strict sympatry.

In a wider sense, so as to include the cases of some species collected together

^{***} For further details on gonads of H. kiiensis, see text.

^{****} Having big space within mantle wall; for details, see text.

^{*****} Ejectors issuing from axial vas deferens.

from the same stations as sympatry, there are examples of sympatric occurrence of H. momus and H. pallida in the Gulf of Suez (including the type-series of Pyura momus f. kyamenensis; see Appendix), in Tahiti (including the type-series of Cyn-thia papietensis; ditto), and at Hatakejima Is., Tanabe Bay, Kii Peninsula, Japan; for H. momus and H. japonica in the Oki Isls, Sea of Japan; and for H. momus and H. kiiensis in Nigijima-cho, Kii Peninsula, Japan. These examples provide clues for studying the course of speciation in this genus.

Classification of *Herdmania* species

Japanese and some other species of the genus *Herdmania* are distinguishable from one another as follows. Only *H. columna* Monniot and Monniot, 1991 from New Caledonia (Monniot and Monniot 1991: 413–416) has several gonads on each side. *Herdmania armata* Monniot and Monniot, 2001 from Papua New Guinea (Monniot and Monniot 2001: 337–339) has a single gonad on each side, but each gonad consists of several capsules. Table 2 shows the diagnostic features of the species that have a single massive gonad on each side. Of such species, *Herdmania mauritiana* is unique in having a filament-born membrane on each side of the aperture of the vas deferens, which opens at the tip of a short, free tube. *Herdmania inflata* is also peculiar in having a long anterior stalk of the tunic, which includes a mantle extension.

Other than the many species referred to in the present study, there may be additional distinct species of *Herdmania* outside Japanese waters, which have been treated as junior synonyms of *H. momus* or confused with other species. Further examination of name-bearing types and other museum specimens will contribute to our better understanding of the taxonomy and diversity of this genus.

Acknowledgements

I dedicate this paper to the memory of the late Dr. Takasi Tokioka, recently deceased at the age of 87 on 30 September 2001, with my heart-felt gratitude for his consistent guidance and encouragement of my taxonomic work. I would like to express my cordial gratitude to C. and F. Monniot (Muséum national d'Histoire naturelle, Paris) for a copy of Bouchet and Danrigal's (1982) paper, loan of type specimens, helpful information, and a copy of the accepted manuscript of their own paper published in 2001; to the two reviewers for improvement of the manuscript; to H. Ruhberg and P. Stiewe (Zoologisches Institut and Zoologisches Museum, Universität Hamburg), P. Bartsch and K. Meschter (Museum für Naturkunde der Humboldt-Universität zu Berlin), H. Sattmann (Naturhistorisches Museum Wien). and A. Pierrot-Bults and J. Bleeker (Zoologisch Museum, University of Amsterdam) for their kind help during my stays at their respective museums and for loans of specimens; to G. Lambert (California State Univ.) and P. Kott (Queensland Museum) for information; to P. Berents (Australian Museum, Sydney), S. H. Halsey (The Natural History Museum, London), H. Namikawa (National Science Museum, Tokyo), M. Michikawa (Univ. Tsukuba), L. Cole (National Museum of Natural History, Smithsonian Institution), and C. Nielsen (Zoologisk Museum, Copenhagen) for loans of specimens. Sincere thanks are also due to M. J. Grygier (Lake Biwa Museum) for his critical reading of the manuscript, to M. Nozaki (The Nagoya University Museum) for thin sections and SEM images, to H. Arkwright (The Newcastle University Library) for detailed bibliographical information about Lahille's (1888) paper, to S. Taniguchi and Y. Aoki (Graduate School of Human Informatics, Nagoya Univ.) for technical assistance, further to D. Colombera, R. Fukao, K. Hayashi, Y. Hirose, T. Imaoka, H. Ishii, M. Kashihara, J. Kobayashi, T. Kuwamura, H. Michibata, F. Nakaya, S. Ooishi, M. Ootani, H. Saito, T. Shinya, I. Soyama, J. Tsukahara, K. Ueda, H. Yamamoto, K. Yamazato, T. Yasuda, the Noto Marine Biological Station of Kanazawa Univ., the Seto Marine Biological Laboratory of Kyoto Univ., the Shimoda Marine Biological Center of Univ. Tsukuba, the Izu Oceanic Park, and the Sabiura Marine Park Research Laboratory, for material and/or help in collecting specimens. This study was supported financially in part by a Grant-in-Aid for International Scientific Research (No. 09041155, headed by TN) from the Ministry of Education, Science, Sports and Culture, Japanese Government, a Grant-in-Aid for Scientific Research (B) (No. 12575008, headed by S. F. Mawatari of Hokkaido Univ.) from the Japan Society for the Promotion of Science, and the Nagoya University Foundation in 2001.

Appendix Lectotype Designations in the Present Study

1. Pyura momus f. kyamanensis Michaelsen, 1919

BZM 3315 is part of the syntype lot represented by "mehrere Stücke" (in the original description) from Umm el Kyaman (Umm el Jerman), Gulf of Suez, collected by R. Hartmeyer, 18-20 Jan. 1902; included are five glass vials, four of which include numbered labels, and two intact ascidians, probably *Pyura tessellata*; the fragmented specimen in vial #26 is designated as the lectotype because it has a gonadal structure similar to that shown in Michaelsen (1919, pl. 1, figs 19–20) for Pyura momus f. kyamanensis and identified in the present study as Herdmania pallida; the paralectotype fragmented specimens in vials #28 and #33 are identified as H. momus. ZMUH T1020, collected from "Rotes Meer, Umm el Kyaman" (cited from the ascidian catalog of ZMUH), is lost. The label of NMW Mollusken Sammlung Nr. 55606, "Pyura momus (Sav.) f. jermanensis Michaelsen, Cotype!, W. Michaelsen determ. 1917, Dahab, 6.4.1896, 'Pola' Exp.", is very reminiscent of what was written in the original description for a specimen of P. momus f. kyamanensis other than those from Umm el Kyaman (Jerman), that is, "Dahab; Pola-Exp., 6. April 1896 (1 Stuck)". Nr. 55606 consists of a single, 17.3 mm long, already dissected individual. The trinomen P. momus f. jermanensis was never published, and Nr. 55606 may well be regarded as another syntype of P. momus f. kyamanensis. My examination of the specimen revealed some siginificant differences from the lectotype, probably meriting assignment to a new species of *Herdmania*.

2. Cynthia papietensis Herdman, 1882

According to the original description, the syntypes comprised seven specimens collected from Papiete (i.e. Papéeté) Harbor, Tahiti, Society Isls, 28 Sept. 1875, during the "Challenger" Exp., at depths of 10 and 20 ftms (i.e. 18 and 36 m). The only already dissected specimen among the five syntypes (NHML 1887.2.4.63–67), an individual 20 mm long, is designated as the lectotype. This may be the specimen that was collected at a depth of 10 fathoms (i.e. 18 m) and whose external appearance in the original description (Herdman 1882, pl. 17, fig. 11) led to its identification in the present study as *H. momus*. The remaining four syntypes of that lot, together with a single 12 mm long specimen (ZMB 3094) that remained intact until my exmina-

tion, are paralectotypes of *C. papietensis*; the ZMB specimen, collected at depths of "10–20 F." (cited from the specimen label) proved to belong to *H. pallida*. The present location of the seventh syntype (i.e. the sixth paralectotype) of *C. papietensis* is unknown.

3. Cynthia pallida Heller, 1878

According to the original description, the type series came from "Mauritius (Prof. Möbius), Jamaika (Prof. Schmarda), Huahine, Palau, Tahiti (Mus. Godeffroy)". Among these, the present location of the specimen(s) from Tahiti is unknown; the material from Palau was once registered as ZMUH T77 but has been lost. The 39 mm long individual from Jamaika (i.e. Jamaica) (NHMW Mollusken Sammlung Nr. 57788) is represented by its tunic. The 27 mm long, already dissected specimen (NHML 1914.5.18.26) labeled as "Co-TYPE of *Pyura pallida* (Heller), Fouquet Id., Berlin Museum Exchange, Möbius", and obviously coming from Fouquet Is. off the east coast of Mauritius, is assignable to the genus *Cnemidocarpa*. All these specimens should be excluded from consideration for lectotype designation.

The material of ZMB 704 from Mauritius consists of three specimens, of which one 41 mm long remains intact, and one 31 mm long lacks the mantle body. The remaining, already dissected, 31 mm long specimen is designated as the lectotype of *Cynthia pallida* Heller, 1878 for stability of zoological nomenclature, because the material from Huahine (ZMUH T78) was unallotable to any known species of *Herdmania*. Since Mauritius is mentioned firstly in the original description, it seems appropriate for this to become the sole type locality.

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